

VARIABILITY IN BROODING ACTIVITY IN THE STALKED BARNACLE *POLLICIPES POLYMERUS*

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ABSTRACT

Reproductive activity in the barnacle, *Pollicipes polymerus*, was studied at sites along the west coast of North America and in the laboratory. Patterns of seasonal brooding activity reveal two physiological races: a northern one with maximum brooding activity at cold seawater temperatures (14°C or less) and a southern one which broods most at warmer temperatures (20°C). The distribution of these two races corresponds, respectively, to the cold and warm temperate zones located north and south of Point Conception.

Laboratory experiments support field results that the northern physiological race broods at lower temperatures than the southern physiological race and that seasonal brooding activity is controlled more by water temperature than by food. A specific temperature level does not account for the onset of seasonal brooding activity as well as does a change in temperature toward the optimum level for each physiological race. A possible reason that food does not regulate seasonal reproductive activity in *P. polymerus* is that this large species has sufficient food reserves as compared with smaller barnacles found at higher intertidal levels.

INTRODUCTION

Pollicipes (Mitella) polymerus, Sowerby, 1833, is the common intertidal stalked barnacle along the Pacific coast of North America from Susk, British Columbia (Pilsbry, 1907), to Punta Santa Dominga, Baja California Sur (personal observations). Reproductive activity in this and other intertidal invertebrates varies with space and time and has been attributed to environmental and genetic differences. Previous researchers have studied seasonal reproductive activity in *P. polymerus* by determining the percentage of adults brooding. They noted that periods of high brooding activity correspond with changes in water temperature. Brooding at sites in the cold temperate zone north of Point Conception is greatest during the summer (Hilgard, 1960; Cimberg, 1973; Hand *et al.*, 1973; Lewis, 1975a), whereas in the warm temperate waters south of Point Conception brooding increases during the winter (Straughan, 1971; Cimberg, 1973). This seasonal shift suggests that brooding occurs at an optimal temperature (Cimberg, 1973; Hand *et al.*, 1973), perhaps around 14°C (Cimberg, 1973), reached during summer in the cold temperate and during winter in the warm temperate.

An alternative hypothesis is that some other variable (such as food), which correlates with water temperature, could be the proximal environmental stimulus that triggers the onset of seasonal reproduction. Plankton abundance regulates

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seasonal reproductive activity in several barnacle species (Hines, 1978) and increases during the spring as *P. polymerus* broods at Friday Harbor (Lewis, 1975a).

Reproductive activity varies on a small spatial scale with changes in tidal level in barnacles (Crisp, 1950, 1959) and other invertebrates. This might occur in *P. polymerus*. On a larger spatial scale, variability in reproductive activity within a species whose populations are geographically separated and exposed to different environmental conditions has been attributed to genetic differences (Sastry, 1975). Such variability might occur between populations of *P. polymerus* from the warm and cold temperate zones.

This study further investigated patterns of and factors regulating reproductive activity in the barnacle *P. polymerus*. Answers to the following questions were sought: (1) Does seasonal reproductive activity at sites in both the cold and warm temperature zones fit the model of an optimal temperature for brooding activity? (2) Does water temperature, more than food, control seasonal reproductive activity? (3) What is the relative importance of tidal exposure on reproductive activity? (4) Is there reproductive evidence for genetic differences between populations?

MATERIALS AND METHODS

Field studies

Seasonal brooding activity was studied at a cold temperate site near the Pismo Beach pier (35.10° N, 120.37° W) and at warm temperate sites at Bird Rock, Santa Catalina Island, (33.21° N, 118.20° W) and at Latigo Point (34.02° N, 118.38° W) (Fig. 1) during 1972–1977. *P. polymerus* was sampled throughout the

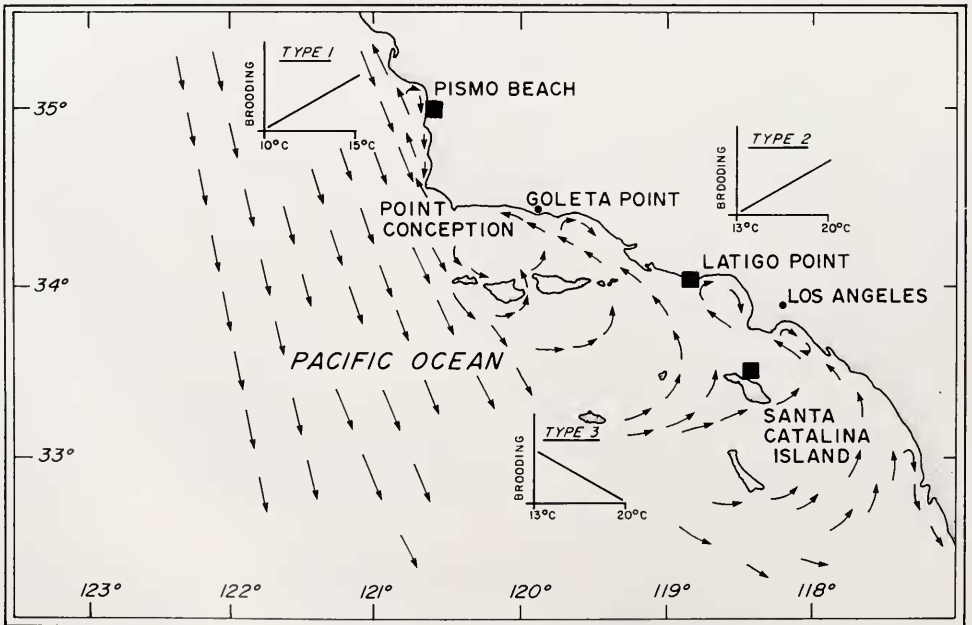


FIGURE 1. Map of the region around Point Conception, California, showing study sites (solid squares) and nearshore current patterns during the oceanic and upwelling seasons (after Pirie *et al.*, 1975).

year. Each sample consisted of a cluster of 10–20 adults with a capitulum height (base of lower latera to tip of tergum) greater than 12 mm, the minimum size at which brooding usually occurs (Barnes and Reese, 1960; Straughan, 1971; Cimberg, 1973). Only animals from clusters were sampled, to insure that cross-fertilization could have occurred. The effect of tidal exposure on brooding was investigated by taking samples from different intertidal levels. The *Pollicipes* zone (that portion of the intertidal region inhabited by adult *Pollicipes*) was divided into two equal vertical sections; 1–4 samples were taken from both the upper and lower levels, thereby totaling 20–160 animals sampled per month at each site. In the laboratory, animals were dissected and the percentage of adults brooding was determined for each sample.

Water temperature data for the respective sites were collected from nearby shore stations: for Pismo Beach, from daily readings at Port San Luis (Physical and Chemical Oceanographic Data Facility, Scripps Institute of Oceanography, unpublished data); for Santa Catalina Island, from daily readings at the Catalina Marine Science Center pier for 1972–1974 (Catalina Marine Science Center, unpublished data) and from weekly means taken from the kelp bed canopy at Bird Rock for 1976 (James Coyer, University of Southern California, personal communication); and for Latigo Point, from daily measurements at Zuma Beach County Park (Los Angeles County Department of Parks and Recreation, unpublished data).

As an alternative to measuring plankton abundance, body weights of barnacles have been used to estimate food reserves (Barnes *et al.*, 1963; Hines, 1978). In this study the soft tissues of the capitulum and peduncle were dissected from their respective external shells and cuticular sheaths and dried at 60°C to constant weight. These weights were standardized for size by dividing by the cube of the rostral-carinal length (Lewis, 1975a), which eliminated the effect of size (Cimberg, unpublished data). Body weights were determined for Santa Catalina Island and Latigo Point animals sampled in 1976 during March, June, October, and December. Using a stratified random method to sample the entire tidal range which *P. polymerus* inhabits, a total of 335 animals were collected from the two sites.

Laboratory experiments

Laboratory experiments were conducted in nine 21-l aquaria in which temperature and food could be varied independently. Each tank was equipped with a bubble curtain to provide vigorous and uniform circulation and a heater to maintain the temperature at the desired experimental level ($\pm 1^\circ\text{C}$). Food abundance was regulated daily in each tank by adding a specified amount of freshly hatched brine shrimp nauplii (*Artemia salina*). All experiments were run under a 12 h light/12 h dark cycle. Seawater was collected on the Palos Verdes Peninsula of Los Angeles, filtered through 0.22 μm Millipore filters, and stored at 6°C in glass containers. To control bacterial growth, seawater was changed every 5 days and Maracyn antibiotics (5 mg minocycline and 100 mg erythromycin) were added daily.

Experimental animals were collected from the middle of the *Pollicipes* zone by chipping off pieces of rock or mussel to which the barnacle clusters were attached. These animals were placed in each tank so that their feeding apparatuses faced into the water current. The animals were maintained for 24 h at the temperature at which they were collected. During the subsequent 7 days, the temperature of each tank was gradually changed to the prescribed experimental level. Each experiment ran for 30 days, after which the percentage of adults brooding was de-

terminated. Because development of the brooding embryos takes 20–31 days (Lewis, 1975b), nearly all embryos present at the end of the experimental period would have been deposited in the mantle (brood) cavity under laboratory conditions.

Two experiments were conducted. Experiment 1 was designed to measure the relative importance of temperature and food on brooding. Three temperatures (10, 15, and 20°C) were tested in combination with three different daily rations of food in the ratio of 0:1:4. This experiment was conducted from 12 October through 10 November 1976, using Pismo Beach animals. Experiment 2 tested for genetic differences, by comparing brooding responses to the same temperatures in animals from two different sites. Each tank received the same amount of *Artemia*, but was set at a different temperature: 8, 10, 12, 14, 16, 18, 20, or 22°C. This experiment was conducted from 18 July to 16 August 1977, using animals from Santa Catalina Island and La Jolla. La Jolla animals (32.50° N, 117.17° W) were used in place of Latigo Point barnacles since not enough experimental animals could be collected from the latter site.

RESULTS

Field studies

Brooding at both tidal levels was compared with water temperature and season (Fig. 2). Although brooding cycles at each site corresponded both with water temperatures (based on a Spearman rank correlation coefficient; Nie *et al.*, 1975) and season, these results differed among sites. At Pismo Beach, brooding occurred during the summer and was highest at 15°C, since brooding activity increased significantly at water temperatures between 12 and 15°C ($r_s = +0.5070$, $N = 104$, $P < 0.001$), but decreased significantly at temperatures above 15°C ($r_s = -0.6187$, $N = 10$, $P < 0.05$). At Latigo Point, which is exposed to warmer temperatures than Pismo Beach, barnacle brooding was highest during the summer and increased significantly as temperatures increased and approached 20°C ($r_s = +0.4666$, $N = 136$, $P < 0.001$). Finally, at Santa Catalina Island, where water temperatures are comparable to those at Latigo Point, brooding was highest during the winter, increasing significantly as temperatures decreased and approached 13°C ($r_s = -0.4897$, $N = 183$, $P < 0.001$). Comparisons of yearly reproductive cycles at Santa Catalina Island showed that a sharp increase in brooding activity each fall corresponded more closely to a change in water temperature than to any particular temperature level (Fig. 2). This fall increase occurred when temperature declined from 18 to 16°C in 1973 as compared to 21 to 19°C in 1976.

Maximum brooding in the higher and lower portions of the *Pollicipes* zone occurred during the same season at each respective site. However, other aspects of the reproductive cycle differed with tidal elevation (Fig. 2). Brooding was significantly greater in the lower than higher portion of the *Pollicipes* zone at Pismo Beach (+15%, $N = 14$, $P < 0.05$), Latigo Point (+14%, $N = 17$, $P < 0.05$), and Santa Catalina Island (+17%, $n = 31$, $p < 0.05$), based on a *t* test for paired comparisons (Nie *et al.*, 1975). In addition, populations brooded earlier in the year and for a longer duration at lower tidal elevations at each site.

Body weights, analyzed using Duncan's multiple range test (Nie *et al.*, 1975), varied significantly ($P < 0.05$) during the year at each site (Fig. 3). Values at Latigo Point were significantly greater ($P < 0.05$) in October than in March, June, or December, whereas at Santa Catalina Island body weights were significantly greater ($P < 0.05$) in June than during the other 3 months.

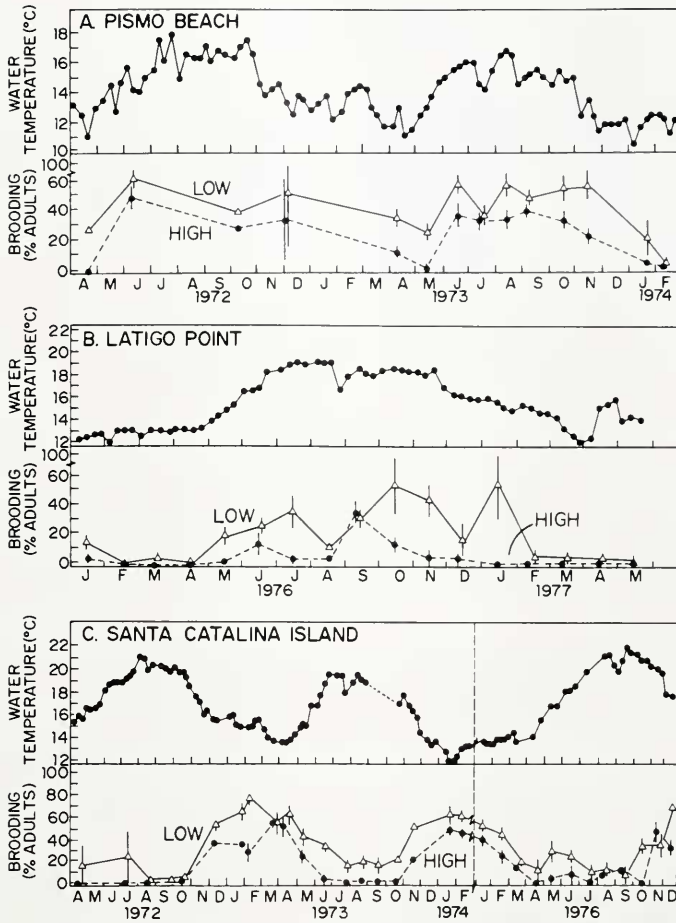


FIGURE 2. Comparison of seasonal brooding activity with average weekly seawater temperatures for populations of *Pollicipes polymerus* at Pismo Beach (A), Latigo Point (B), and Santa Catalina Island (C). Vertical lines represent standard error of the means for high (circles) and low (triangles) intertidal samples.

Changes in brooding activity at each site were compared with water temperature and body weights to determine the relative importance of these two factors on brooding in the field (Fig. 3). Brooding at Latigo Point was greatest when both temperature and food reserves were highest. Brooding at Santa Catalina Island occurred as food reserves were low, but as temperatures approached the optimum level. Correlation coefficients (Spearman rank) were calculated between brooding activity and each of these two independent variables, using data from both sites combined. Brooding was correlated more strongly with a change in temperature, toward the apparent optimal level ($r_s = +0.29$), than with body weight ($r_s = +0.22$).

Laboratory experiments

Results of experiment 1 (Fig. 4) indicated that water temperature had a greater effect on brooding than did food abundance. Food affected brooding under some

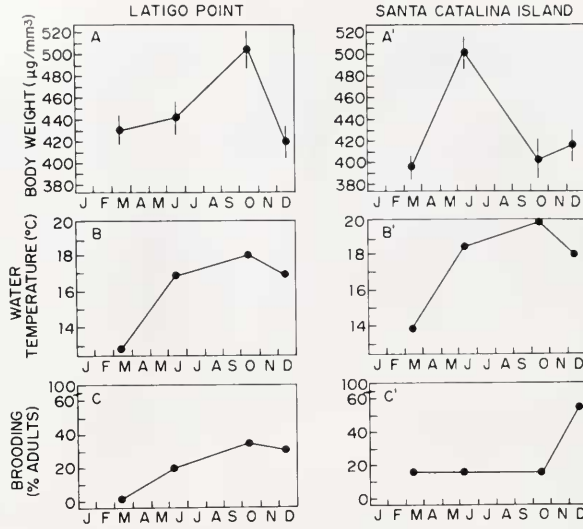


FIGURE 3. Comparisons of *Pollicipes polymerus* brooding activity with seawater temperature and body weight (means and standard errors) at Latigo Point (A, B, C) and Santa Catalina Island (A', B', C').

conditions: unfed animals did not brood, and at the temperature of maximum brooding activity (10°C) food had a significant effect ($\chi^2 = 8.04$, DF = 2, $P < 0.05$). But for all temperatures combined, the effect of food was not significant ($\chi^2 = 5.33$, DF = 2, $P < 0.05$). On the other hand, water temperature had a significant effect on brooding ($\chi^2 = 11.14$, DF = 2, $P < 0.005$) for all food levels combined. Results of experiment 2 (Fig. 5) indicate that barnacles from La Jolla and Santa Catalina Island responded significantly differently ($P < 0.05$) to the same water temperatures, based on a Kolmogorov-Smirnov test (Sokal and Rohlf, 1969); Santa Catalina Island barnacles brooded at significantly lower temperatures than animals from La Jolla.

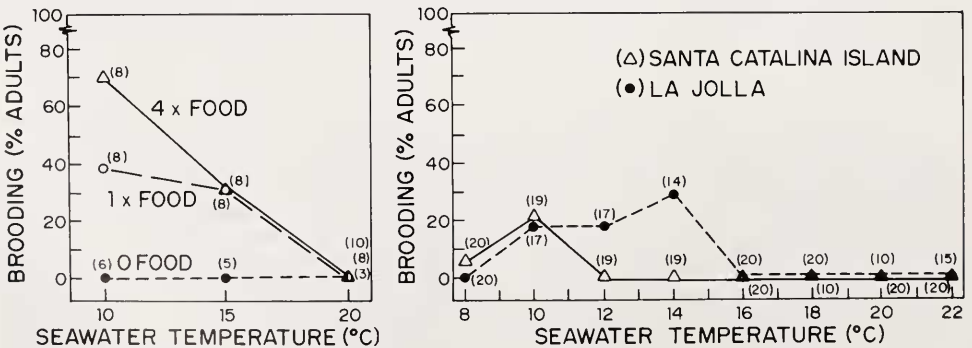


FIGURE 4. (Left) Results of experiment 1, testing the effects of water temperatures (10, 15, and 20°C) and food abundance (in the ratio 0:1:4) on brooding activity of *Pollicipes polymerus* from Pismo Beach, California. Numbers in parenthesis represent sample size per treatment.

FIGURE 5. (Right) Results of experiment 2, comparing brooding responses of La Jolla and Santa Catalina Island populations of *Pollicipes polymerus* to the same water temperatures. Numbers in parenthesis represent sample size per treatment.

DISCUSSION

Brooding and water temperature

Brooding at Pismo Beach and Santa Catalina Island occurs as temperatures approach approximately 14°C , supporting the optimum temperature model proposed independently by Cimberg (1973) and Hand *et al.* (1973). Latigo Point, where brooding increases as temperatures approach 20°C , is the first reported site in which brooding of this species does not increase as temperatures approach $\sim 14^{\circ}\text{C}$. Examination of data from all *P. polymerus* studies revealed three types of brooders (Fig. 6). Type 1 animals, located at all sites north of Point Conception, brood most during the summer as temperatures approach $\sim 14^{\circ}\text{C}$. Type 2 barnacles at Latigo Point, south of Point Conception, brood most during the summer as temperatures increase and approach 20°C . Type 3 animals are found at Santa Catalina Island and Goleta Point, also south of Point Conception, but brood most during the winter as temperatures decrease and approach 13°C .

Type 1 and 3 brooders are similar in the temperature ($\sim 14^{\circ}\text{C}$), though not season, at which brooding occurs. Type 3 animals could have been derived from type 1 populations (Fig. 1). Both Santa Catalina Island and Goleta Point are exposed to portions of the south flowing California Current during the oceanic (March through August) and upwelling seasons (July through November) (Pirie *et al.*, 1974). During these periods *P. polymerus* larvae are released into the water north of Point Conception. Since the current has an average velocity of 0.25 m/s (Jennings and Schwartzlose, 1960), the larvae could be transported 1014 km during their 42 day planktonic period (Lewis, 1975b). As the direct distances from Pismo Beach to Goleta Point and Santa Catalina Island are approximately 145 and 385 km respectively, larvae could reach these sites even if the route was indirect and/or the transport slower.

An alternative relationship among brooding types is that the Latigo Point population (type 2) is a southern extension of the cline composed of type 1 populations (Fig. 6). Maximum brooding in this cline occurs at progressively higher temperatures with correspondingly lower latitudes. This theory does not explain why animals at Goleta Point and Santa Catalina Island (type 3), exposed to essentially

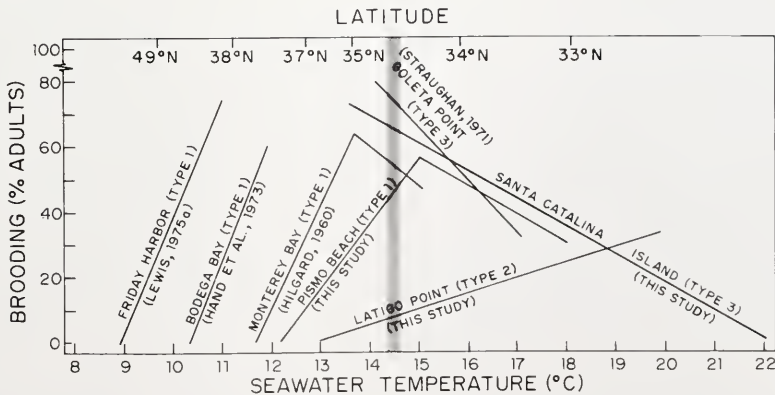


FIGURE 6. Comparison of brooding activity with seawater temperature for *Pollicipes polymerus* populations at sites along the west coast of North America north and south of Point Conception (shaded line).

the same temperatures as Latigo Point animals, have a different pattern and brood during the winter. Nor does it explain why brooding decreases at temperatures higher than $\sim 14^{\circ}\text{C}$ at Pismo Beach and Monterey Bay.

Two kinds of brooders therefore can be identified from this analysis. One, consisting of type 1 and 3 animals, broods at relatively cold temperatures ($\sim 14^{\circ}\text{C}$ or less), regardless of season (Fig. 1); the other, type 2 animals, broods at relatively warm temperatures (20°C). The presence of both kinds of brooders in southern California, exposed to essentially the same water temperatures and yet brooding at different times of the year, indicates genetic rather than environmental differences. Therefore, the cold-water brooders (types 1 and 3) are considered a northern physiological race and the warm-water brooders (type 2) a southern physiological race. Laboratory results indicated that Santa Catalina Island animals (the northern physiological race) brood at significantly lower temperatures than La Jolla barnacles (considered to be of the southern physiological race), even though they are exposed to essentially the same temperatures in the field. This experiment therefore supports field studies regarding the presence of two physiological races.

Physiological races, determined from reproductive studies, have been identified in the American oyster *Crassostrea virginica* (Loosanoff and Nomejko, 1951; Loosanoff, 1969) and the barnacle *Balanus balanoides* (Barnes and Barnes, 1976). Physiological races of these three species, which all have large distributional ranges, occur in different biogeographic provinces. Such races can be difficult to detect, since in *P. polymerus* and *C. virginica*, different races breed during the same season but at different temperatures due to genetic differences; and in *P. polymerus*, the same physiological race will breed at the same temperatures but in different seasons due to environmental differences.

Seasonal brooding and other factors

Brooding at Latigo Point is greatest in October, when body weights are maximal and temperatures apparently optimal. Brooding at Friday Harbor begins in the spring as temperatures and phytoplankton abundance both increase (Lewis, 1975a). Because both factors change at the same time at these sites, their relative importance is difficult to determine. Santa Catalina Island represents a good natural field experiment in that maximum brooding occurs in the winter when food reserves are minimal but temperatures apparently favorable. Correlation coefficients from field data indicate that seasonal brooding corresponds to changes in water temperature better than to changes in food reserves. Laboratory experiment 1 supports field results that temperature has a greater effect than food on seasonal brooding.

The relative importance of water temperature and food on the reproduction of various eastern Pacific, warm temperate, littoral barnacles has an interesting relationship with tidal elevation. Brooding activity in the highest intertidal barnacle (*Chthamalus fissus*) is regulated by food abundance; temperature has no significant effect (Hines, 1978). This species, the smallest of the four common intertidal barnacles along this coast, begins to die after 2 weeks without food in the laboratory (Diane Perry, University of Southern California, personal communication), indicating low food reserves. Seasonal reproduction of the lower barnacle (*Balanus glandula*), is controlled by low seasonal temperatures (Hines, 1978). This larger species lives longer than *C. fissus* when starved (Diane Perry, personal communication), which suggests the presence of greater food reserves. These reserves are stored before and then depleted during the brooding season (Hines, 1978), indicating that food abundance might affect brooding. Seasonal reproduction in the

two lowest intertidal barnacles is regulated by water temperature; both *P. polymerus* (this study) and *Tetraclita squamosa* (Hines, 1978) breed at an optimal temperature, and are apparently not affected by food abundance. These two species are larger than the others and have greater nutrient reserves; *P. polymerus* can live for at least 4 weeks without food (this study), and nutrient storage in *T. squamosa* does not decrease during the reproductive season (Hines, 1978). Thus, the larger barnacle species along the coast inhabit lower tidal elevations and apparently store greater food reserves. Greater nutrient storage may explain why food is less important than water temperature in regulating seasonal brooding in these species than in smaller barnacles at higher tidal levels.

Light influences seasonal reproduction in the barnacle *Balanus balanoides*, (Barnes, 1963) and inhibits *P. polymerus* feeding in the laboratory (personal observations). However, light does not appear to be the primary factor controlling *P. polymerus* seasonal reproduction, since populations at Latigo Point and Santa Catalina Island, essentially at the same latitude and exposed to the same light regimens, brood 6 months apart.

Temperature control of reproduction

The factor triggering the onset of seasonal brooding might not be a specific water temperature but a change in temperature. Brooding at Santa Catalina Island increased sharply each fall at different temperature levels, but always with a temperature decline. Brooding at sites north of Point Conception occurred at different temperatures, but always as temperatures changed towards an optimum. Maximum brooding at Santa Catalina Island and Pismo Beach did not occur at the same temperatures in the laboratory as in the field for the respective sites, but did occur with a change in temperature. Brooding in *P. polymerus* therefore could be regulated by a change in temperature, as has been found in the reproductive processes of other marine invertebrates (Giese and Pearse, 1974). The possibility that a temperature change might control brooding activity does not preclude the presence of physiological races reproducing at different temperatures. It does indicate that such a triggering mechanism operates within the individual activity ranges of each race. A change of temperature towards an optimum is therefore hypothesized to trigger the onset of seasonal brooding in each race.

The season of maximum reproductive activity can change with a shift in the time of year when the optimal temperature for brooding occurs. Santa Catalina Island and Goleta Point populations of *P. polymerus* breed 6 months apart from populations north of Point Conception, but as temperatures approach the same level (Fig. 1). The same shift is noted between populations of the northern anchovy *Engraulis mordax* found north (Richardson, 1973) and south (Brewer, 1978) of Point Conception. On a smaller geographic scale, the barnacle *Tetraclita squamosa* normally broods during the summer in Morro Bay as temperatures approach 15°C (Hines, 1978), but 2 miles away near a thermal outfall (13°C above ambient) these barnacles brood in the winter when decreasing temperatures approach 15°C. Finally, *P. polymerus* populations located further south at Punta Santa Dominga, Baja California Sur, brood at approximately 20°C during the winter (Cimberg, unpublished data), 6 months out of phase with, but at the same temperatures as, populations of the southern race at Latigo Point.

Brooding activity and tidal elevation

Maximum brooding activity of *P. polymerus* occurs during the same season for both high and low intertidal populations at each site, but the percentage of adults

brooding was significantly greater per month at lower than higher tidal elevations. Although Lewis (1975a) reported no significant differences in the percentage of adults brooding at different tidal elevations at Friday Harbor, a recalculation of her data using a *t* test for paired comparisons (Nie *et al.*, 1975), during the months in which brooding did occur, shows that brooding activity is significantly greater (+9% difference, $P < 0.05$) at lower tidal levels. Animals at lower tidal elevations also brood earlier and during more months of the year at each site in the present study. Populations at Santa Catalina Island and Pismo Beach brood throughout the year at lower elevations, but only during part of the year at higher intertidal levels.

The relationship between the level of the intertidal in which brooding first occurs in *Pollicipes* and other invertebrates, and the factor that regulates seasonal reproductive activity, suggests that changes in reproductive activity with both space and time could be due to the duration and intensity of a single factor. The barnacle *Chthamalus stellatus* (Crisp, 1950), the clam *Hiatella* (Hunter, 1949), and the limpet *Acmaea scabra* (Sutherland, 1970) all breed earlier at lower than higher tidal levels. Seasonal reproductive activity in *C. stellatus* (Patel and Crisp, 1960), *Hiatella*, *A. scabra*, and *P. polymerus* (this study), is controlled by temperature and/or food abundance. In contrast, seasonal reproductive activity in the barnacle *Balanus balanoides* occurs earlier at high tidal elevations (Crisp, 1959) and is influenced by light (Barnes, 1963) and possibly air temperature (Barnes and Barnes, 1976). Therefore, the onset of reproductive activity in these species occurs initially in that level of the intertidal zone having the longest exposure (duration) to the factor(s) that controls seasonal reproductive activity. In turn, seasonal reproductive activity in these species occurs with changes in the intensity (dosage) of the controlling factor(s). Therefore, patterns of reproductive activity at a single locality occur with space (tidal height) and time (season) and could be regulated, respectively, by the duration and intensity of the controlling factor.

Biogeography of races

For many taxa, Point Conception is a biogeographical boundary between the cold and warm temperate zones (Brusca and Wallerstein, 1979). Newman (1979) noted that of all 26 species of near-shore temperate barnacles, *P. polymerus* is the only species whose northern or southern limit does not end near Point Conception; however, this study indicates that the distribution of the two physiological races of *P. polymerus* is interrupted there. Electrophoretic studies indicate that this area also acts as a boundary between genetically dissimilar populations of the isopod *Ligia occidentalis* (McGill, 1978) and the sculpin *Clinocottus analis* (Swank, 1979).

The distribution of the *P. polymerus* races is associated with the warm and cold temperate waters; however, offshore populations on Santa Catalina Island are exposed to essentially the same water temperatures as Latigo Point animals on the mainland, but are genetically more similar (based on reproductive studies) to populations in colder waters north of Point Conception. Similar results based on electrophoretic patterns were reported for populations of *C. analis* (Swank, 1979) and *L. occidentalis* (McGill, 1978). These offshore islands are exposed to currents originating from cold waters north of Point Conception (Fig. 1) but have temperatures similar to those along the southern California mainland. Thus, at certain sites in the transition zone between the two regions, the distribution of these races

corresponds better to current patterns, which affect larval dispersal, than to temperatures, which affect the adult's physiology.

The relationship between temperatures within a species' biogeographic range and temperatures for reproduction has been noted by Hutchins (1947). He hypothesized that the minimum and maximum temperatures for reproduction among northern hemisphere shallow water species corresponded, respectively, with the summer temperatures at the northern boundary and the winter temperatures at the southern boundary. Molluscan data (Golikov and Scarlato, 1973) supports this model; the Pacific-Asiatic-low-boreal (cold temperate) species reproduce between 6 and 14°C, whereas the Pacific-Asiatic-subtropical-low-boreal (warm temperate) species reproduce between 14 and 20°C. Field data indicate that *P. polymerus* populations of the cold temperate race brood most actively between 11 and 14°C, and the warm temperate race broods at 20°C. Field data near the distributional boundaries are needed to determine more accurately the entire temperature range of brooding activity for populations of both races.

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